

Hatching phenology of Odonata species inhabiting temporary and permanent water bodies (Odonata: Lestidae, Aeshnidae, Libellulidae)

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The hatching phenology of 15 Odonata species was studied under seminatural conditions to find out how the hatching modes of typical species of summer dry temporary waters (vernal ponds) differ from those of species inhabiting both permanent and temporary waters. We attempt to answer the following questions. (1) Do vernal pond species hatch earlier in the year than congeneric permanent water species? (2) Can hatching in vernal pond species be delayed under unsuitable environmental conditions, like drought? (3) Can eggs of vernal pond species survive for more than one year? Larvae of vernal pond species, *Aeshna affinis*, *Lestes barbarus*, *L. dryas* and *Sympetrum flaveolum*, hatched significantly earlier than their permanent water counterparts *A. mixta*, *L. sponsa*, *L. virens*, *L. viridis*, *S. danae*, *S. depressiusculum*, *S. meridionale*, *S. sanguineum*, *S. striolatum* and *S. vulgatum*. Only one vernal pond species, *L. macrostigma*, did not show this early hatching. In both vernal pond and permanent water species hatching succession of different clutches of each species varied, which may reflect genotypic differences. In both vernal pond species and permanent water species hatching was delayed when eggs were kept on moist filter paper – simulating drought – instead of being put into water. The hatching success of two vernal pond species and of four out of five studied permanent water species was reduced significantly by keeping eggs on moist filter paper. Survival of eggs for more than one year could not be proved under temperature conditions resembling those in nature.

Keywords: hatching phenology; temporary water; delayed development; life history; *Lestes*; *Aeshna*; *Sympetrum*; temperate climate; hydroperiod; dragonfly

Introduction

Duration of embryonic development is determined by two events: completion of embryonic development and hatching (Corbet, 1999). Hypoxia, light, water contact, and water temperature can work as stimuli which influence the time of hatching (Corbet, 1999, p. 52). Under arid subtropical climate conditions, Odonata species inhabiting temporary waters usually show direct development, without a diapause in the egg and larval stage. This is interpreted as an adaptation to reach emergence before the larval habitats dry out (Corbet, 1999, p. 52; Suhling, Jödicke, & Schneider, 2003; Suhling, Schenk, Padeffke, & Martens, 2004). By contrast, the eggs of many temperate-centred Odonata species exhibit delayed development, with diapause acting

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as a mechanism to protect early larval stadia from low winter temperatures (Corbet, 1999, p. 56). Species showing only delayed development are known in six genera of Odonata (Corbet, 1999, p. 52), of which species of *Aeshna*, *Lestes* and *Sympetrum* predominate in European temporary water bodies. Two factors, with opposite effects, are likely to affect the timing of hatching in temperate-centred Odonata species adapted to summer dry temporary ponds (hereafter termed vernal ponds). On the one hand, these species have to avoid low temperatures because early larval stadia of Odonata are generally thought to be sensitive to low temperatures (Corbet, 1999). Therefore, hatching is expected to happen only after water temperatures have reached a specific threshold value. On the other hand, larvae of univoltine species typical of vernal ponds ought to hatch early in the year, because the time for larval development is restricted due to the short time that these ponds contain water. This trait has already been demonstrated for *Lestes viridis* by De Block, Stoks, and De Bruyn (2005): in populations of temporary ponds hatching took place earlier in the year than in populations of permanent ponds, the differences not being genetically fixed.

Little is known about the hatching phenology of European Odonata species with egg diapause. In order to identify mechanisms enabling typical inhabitants of vernal ponds to survive under the specific conditions of their habitats, the hatching phenologies of five European vernal pond species, namely *Aeshna affinis*, *Lestes barbarus*, *L. dryas*, *L. macrostigma*, and *Sympetrum flaveolum*, were compared with those of their permanent water congeners. In total we investigated 15 species under different conditions measuring timing of hatching and hatching success. We aimed to answer the following three questions:

- (1) Do typical vernal pond species hatch earlier in the course of the year than congeneric permanent water species?
- (2) Can hatching in vernal pond species be delayed under unsuitable environmental conditions, like drying of the larval habitat?
- (3) Can eggs of vernal pond species survive for more than one year?

Material and methods

In our study we compared the hatching phenology of *Aeshna affinis*, *Lestes barbarus*, *L. dryas*, *L. macrostigma*, and *Sympetrum flaveolum*, all specialized to summer dry temporary waters, with congeners which are less specialized and can develop both in permanent and temporary waters including vernal ponds. For convenience we term the specialized species in the following “vernal pond species” and the less specialized species “permanent pond species”. The permanent pond species included *A. mixta*, *L. sponsa*, *L. virens*, *L. viridis*, *S. danae*, *S. depressiusculum*, *S. meridionale*, *S. sanguineum*, *S. striolatum*, and *S. vulgatum*. We were not able to obtain eggs of all species simultaneously. Therefore, the study was carried out from 2005 to 2011 (Table 1).

Eggs of Anisoptera species were obtained by catching copulating or ovipositing females. Eggs of *Sympetrum* species, which oviposit exophytically, were easy to obtain by dipping the female's abdomen into a tube with water (see Boehms, 1971; Robert, 1959) or – in the case of *S. sanguineum* and *S. flaveolum* – onto a moistened piece of filter paper. Females of the two *Aeshna* species, with endophytic oviposition, were forced to lay their eggs in captivity into tissue paper. Eggs of *Lestes* species were collected from their oviposition plant tissues *in situ* (cf. Corbet, 1956a; Sawchyn & Church, 1973). Eggs of all species were collected at different sites in south-western Germany (in a range of 47°50' N to 49°11' N), those of *S. flaveolum* additionally at a karst elevated plain in Umbria, Central Italy (42°46' N). Stems of *Bolboschoenus maritimus* containing eggs of *L. macrostigma* were collected by Dr T. Benken in eastern Austria (47°47' N). The Anisoptera eggs were kept in Petri dishes lined with wet filter paper and put onto a moist

Table 1. Number of hatching events in the 15 species for which hatching phenology was studied from 2005/2006 to 2011. In parentheses are numbers of stems in *Lestes* species and numbers of clutches in *Aeshna* and *Sympetrum* species. Species specialized in vernal ponds are indicated in bold.

Species	Year of survey					
	2005–2006	2006–2007	2007–2008	2008–2009	2009–2010	2010–2011
<i>Aeshna affinis</i> Vander Linden, 1820				855 (9)	190 (5)	157 (1)
<i>Lestes barbarus</i> (Fabricius, 1798)	49 (37)	254 (11)			20 (2)	406 (22)
<i>Lestes dryas</i> Kirby 1890						242 (26)
<i>Lestes macrostigma</i> (Eversmann, 1836)					3 (1)	11 (10)
<i>Sympetrum flaveolum</i> (Linnaeus, 1758)	317 (14)			252 (11)	187 (12)	301 (10)
<i>Aeshna mixta</i> Latreille, 1805			452 (3)	681 (7)	198 (2)	
<i>Lestes sponsa</i> (Hansemann, 1823)						154 (5)
<i>Lestes virens</i> (Charpentier, 1825)		207 (10)	899 (20)		1,443 (20)	695 (17)
<i>Lestes viridis</i> (Vander Linden, 1825)						10,357 (17)
<i>Sympetrum danae</i> (Sulzer, 1776)		99 (1)	255 (8)	602 (7)	197 (4)	
<i>Sympetrum depressiusculum</i> (Selys, 1841)	303 (6)	708 (7)	224 (7)	490 (6)	169 (5)	
<i>Sympetrum meridionale</i> (Selys, 1841)		84 (3)				
<i>Sympetrum sanguineum</i> (Müller, 1764)		33 (7)	10 (14)	44 (14)	190 (10)	
<i>Sympetrum striolatum</i> (Charpentier, 1840)		494 (5)	4336 (11)	639 (4)	163 (5)	
<i>Sympetrum vulgatum</i> (Linnaeus, 1758)		1257 (4)	353 (5)	233 (1)	194 (5)	

piece of cotton. Water was added when necessary to prevent desiccation. *Lestes* eggs were kept in the oviposition tissues placed in plastic boxes with a wet piece of cotton to prevent desiccation. We exclusively used rain water to prevent accumulation of soluble salts. The program xlstat2014 (Addinsoft, 2014) was used for all statistical tests. The sampled eggs were subdivided into different fractions for the following experiments.

Comparison of hatching phenology

Eggs of *Sympetrum* and *Aeshna* species were placed in closed Petri dishes filled with 10–30 ml rain water, those of *Lestes* species in uncovered larger plastic boxes containing plant stems

with eggs and filled with 400 ml rain water. Twigs with eggs of *L. viridis* were placed in an open bucket with water-covered bottom; the eggs did not come into contact with water. From 2005/2006 to 2008/2009 hatching phenology was documented clutch-wise for all Anisoptera species. In 2009/2010 and 2010/2011 and generally for *Lestes* species, in which single clutches could not be discriminated, eggs of different clutches were mixed. Altogether 218 clutches of nine Anisoptera were involved and more than 163 stems containing eggs of six *Lestes* species (Table 1). All eggs were kept under outdoor temperature and natural light conditions on an easterly exposed balcony (48°38' N, 8°05' E). The egg containers were kept together in open cardboard boxes placed on the floor. The eggs received direct sunlight only in June until 7:00 a.m. central European time for a time span not exceeding 30 min. Due to the incidence angle of sunrays eggs were not exposed to direct sunlight in any other month. There was no artificial source of light such as streetlamps disturbing natural photoperiod. A possible disturbance of natural photoperiod may have been caused by recording hatching events in the late evening.

The number of freshly hatched larvae was monitored daily, usually in the late evening; during periods with many hatching events additionally in the early morning. The hatchlings were removed from their containers to prevent double counting. In this way, we were able to determine the hatching date of each larva to a precision of one day. These basic data were analysed in three ways to document intraspecific variance both of different clutches and between years, and to compare interspecific differences. To document the degree of intraspecific variance of hatching date we compared clutches gathered from different females of the same species. We considered only clutches collected during a period of at most two weeks to eliminate seasonal effects. To get sufficient data for statistical analysis we decided a priori to analyse only clutches with a minimum of 20 successful hatching events. Because hatching dates of all species differed between years we also compared the inter-annual variance of hatching date. We could not use data from eggs collected in 2006 for this comparison, because they were kept in a refrigerator at constant 5°C and in dark from 8 February 2007 until 30 March 2007 due to a journey abroad by the first author. Suitable data for inter-annual, intraspecific comparison of hatching succession were available for four years in *S. depressiusculum* and *S. flaveolum*, for three years in *A. affinis*, *A. mixta*, *Lestes barbarus*, *L. virens*, *S. danae*, *S. sanguineum*, *S. striolatum*, and for two years in *S. vulgatum*. Since the data were not normally distributed the significance of all comparisons – intraspecific-intra-annual, intraspecific-inter-annual and interspecific – were tested with the non-parametrical Kruskal–Wallis test, followed by a pairwise comparison using the Mann–Whitney U test with Bonferroni adjustment.

We aimed to find out the minimum temperatures at which hatching of single species took place as well as the proportion of hatching events taking place at temperatures below 5°C and 10°C. Both were taken as an indirect measure of median hatching dates. Temperature data for this analysis were measured in 2010 and 2011 with a thermometer placed next to the egg containers. Due to the small water volumes ranging from 10–30 ml in the Petri dishes up to a maximum of 400 ml in the plastic boxes we assumed that the recorded air temperatures outside were a reasonably good approximation of the water temperatures inside the hatching containers. Minimum hatching temperatures refer to the highest recorded temperatures measured in the time span between two hatching examinations. Temperature was measured five times during the day (morning, noon, afternoon, evening, night).

The median hatching dates from *S. depressiusculum* and *S. flaveolum* of each of the four years were correlated with the average diel temperatures from 1 January until the median hatching date of the respective species using Spearman's rank correlation. Average diel temperatures were calculated by summing the daily average air temperatures from the weather station and dividing the sum by the number of days from 1 January and the median hatching date of the respective species in the respective year. We took average diel temperature as independent and

Table 2. Mean temperatures (°C) during the study period from the nearby Deutscher Wetterdienst weather station at Rheinau-Memprechtshofen (48°40' N, 7°59' E).

	January	February	March	April	May	June	July	August	September	October	November	December
2005									16.4	11.3	4.8	1.9
2006	-1.2	1.4	4.6	9.9	14.7	18.8	23.9	16.5	17.6	13.0	8.0	4.7
2007	6.1	6.0	7.1	13.9	16.3	19.0	18.4	18.2	13.3	9.9	4.3	1.8
2008	4.1	4.5	6.1	9.2	16.9	18.5	19.3	18.4	13.4	10.2	5.9	1.8
2009	-2.0	1.8	5.8	12.6	15.9	17.6	19.3	19.9	15.9	9.8	8.5	3.0
2010	-0.9	2.5	5.9	11.0	12.6	18.6	21.2	18.1	13.8	9.0	6.8	-0.9
2011	2.7	3.9	7.7	13.3	16.2	18.4						

median hatching date as dependent variable. Data on daily average air temperatures taken for this correlation were obtained from the nearby weather station of the “Deutscher Wetterdienst” in Rheinau-Memprechtshofen (48°40' N, 7°59' E), which was located about 9 km west of the study site (Table 2).

Hatching delay

To find out if eggs can survive more than one year and if hatching can be delayed under inappropriate conditions, a portion of the eggs was kept in the Petri dishes described above on moist filter paper under natural daylight conditions. The Petri dishes were placed on a balcony under outdoor temperature conditions as well.

This experiment was carried out for the following seven species: *Aeshna affinis* (2009: eggs of nine females), *A. mixta* (2008: seven females), *Sympetrum danae* (2007: eight females; 2009: seven females), *S. depressiusculum* (2006: seven females; 2007: seven females; 2009: six females), *S. flaveolum* (2006: 14 females), *Sympetrum striolatum* (2007: five females), and *S. vulgatum* (2007: four females). The eggs were collected in the respective year prior to the experiment. The eggs from *S. depressiusculum*, *S. striolatum* and *S. vulgatum* collected in 2006 were kept in a refrigerator at 5°C from 8 February 2007 until 30 March 2007; all others were kept completely under natural temperature conditions described above. In *S. flaveolum* and *S. depressiusculum* we varied the experiment by placing one clutch of each, from 18 August 2005 and 3 September 2005 respectively, in water and splitting the eggs of the remaining 14 and six clutches, respectively, into three parts. One third of these were transferred into water on 30 March 2006 under natural daylight conditions, one third kept on moist filter paper under natural daylight conditions, and the last third kept on moist filter paper in a dark box.

Differences in hatching phenology among these three treatments were tested using a Kruskal–Wallis test followed by pairwise comparisons using the Mann–Whitney U test. Differences in hatching success among treatments were tested for each species using a two-sided chi-square test.

Duration of egg survival

All *Sympetrum* eggs collected in 2005 and 2006, in which hatching did not take place in the year after oviposition and which still looked intact, were kept until 15 June 2008. All *Aeshna* eggs collected in 2008 were monitored until 30 July 2009; eggs placed on moist filter paper were transferred into water at the latest in the second season after oviposition (Table 3). A part of the stems with oviposition marks from *Lestes barbarus* and *L. virens* were treated the same way (Table 3). In times without frost these eggs were also examined daily for hatching events. The

Table 3. Numbers of eggs, or of egg marks for *Lestes* species, which were kept for more than one year to find out if eggs can survive for more than one year. In parentheses are numbers of stems in *Lestes* species or numbers of clutches in *Sympetrum* species. Vernal pond species are indicated in bold.

Species	Year of sampling		
	2005	2006	2007
<i>L. barbarus</i>	~ 800 (37)	~ 300 (11)	
<i>S. flaveolum</i>	542 (14)		
<i>L. virens</i>		~ 300 (12)	~ 300 (6)
<i>S. danae</i>		45 (1)	
<i>S. depressiusculum</i>	328 (6)	580 (7)	
<i>S. meridionale</i>		110 (3)	
<i>S. sanguineum</i>		40 (7)	
<i>S. striolatum</i>		100 (5)	
<i>S. vulgatum</i>		150 (4)	
Water transfer at	17 April 2007	1 April 2008	15 June 2008

Table 4. Hatching success of eggs of different species kept in the refrigerator (5°C, dark). Vernal pond species are indicated in bold.

Species	Oviposition date	Number of eggs (clutches/ stems)	Date of watering	Hatching success (%)	Time span in refrigerator (months)
<i>A. affinis</i>	29 July 2009	885 (6)	7 January 2011	0.0	17
<i>L. barbarus</i>	6 August 2010	75 (9)	17 May 2012	0.0	21
<i>L. dryas</i>	5 August 2010	89 (2)	17 May 2012	0.0	21
<i>S. flaveolum</i>	10 July 2009	194 (20)	8 May 2011	0.0	22
<i>A. mixta</i>	31 August/ 24 September 2009	592 (3)	8 May 2011	0.0	20
<i>L. sponsa</i>	5/8 August 2010	80 (3)	17 May 2012	0.0	21
<i>L. virens</i>	12 September 2010	50 (7)	17 May 2012	0.0	20
<i>L. viridis</i>	7 September 2010	100 (2)	17 May 2012	0.0	20
<i>S. danae</i>	7 September 2009	603 (4)	8 May 2011	0.3	20
<i>S. depressiusculum</i>	7 September 2009	200 (2)	17 May 2012	0.0	32
	20 August 2009	300 (6)	8 May 2011	71.7	20
	20 August 2009	379 (6)	17 May 2012	0.0	32
<i>S. sanguineum</i>	7 August 2009	410 (9)	8 May 2011	0.0	21
<i>S. striolatum</i>	5 September 2008	1,595 (2)	26 August 2009	1.1	11
<i>S. vulgatum</i>	5/27/31 August 2009	1,675 (5)	8 May 2011	0.0	20
	5/27 August 2009	200 (4)	17 May 2012	0.0	32

latest transfer into water of eggs collected in 2005 took place on 17 April 2007, of eggs collected in 2006 on 1 April 2008. Furthermore, six stems of *Juncus effusus* with egg marks of *L. virens* collected on 18 September 2007 were transferred into water on 15 June 2008.

To find out whether eggs stay viable for more than one year, a portion of the eggs of 13 species (*Aeshna affinis*, *A. mixta*, *Lestes barbarus*, *L. dryas*, *L. sponsa*, *L. virens*, *L. viridis*, *Sympetrum danae*, *S. depressiusculum*, *S. flaveolum*, *S. sanguineum*, *S. striolatum*, *S. vulgatum*) collected in 2009 and 2010 was kept in Petri dishes on moist filter paper in a dark refrigerator at temperatures of 5°C for time spans ranging from 11 to 32 months (Table 4). After that, we transferred them into water under natural temperature and natural daylight conditions. The number of hatching events was documented for a time span of at least three months after the egg transfer and the proportion hatching was determined for each species.

Results

Comparison of hatching phenology

Hatching patterns of clutches from different females of all five tested species differed significantly (two sided Kruskal–Wallis test, $p < 0.0001$, $\alpha = 0.01$). In a pairwise comparison with two-sided Mann–Whitney U test 0–80% of combinations differed significantly ($p < 0.0001$, $\alpha = 0.0005$, Table 5). As an example, this can be demonstrated for the hatching patterns of *S. flaveolum* and *S. depressiusculum* collected in 2008 (Figure 1; for oviposition dates see Table 5). The intra-specific variance tended to be smaller in the typical vernal pond species *A. affinis* and *S. flaveolum* than in their permanent water congeners *A. mixta*, *S. danae* and *S. depressiusculum*.

Hatching phenology of each of the 10 tested species varied significantly (two-sided Kruskal–Wallis test for each species, $p < 0.0001$, $\alpha = 0.01$) between the respective study years (Figure 2). Variance of the hatching dates between years was larger in the vernal pond species *A. affinis*, *L. barbarus* and *S. flaveolum* than in the late hatching permanent water species *A. mixta*, *L. virens*, *S. danae*, *S. depressiusculum* and *S. sanguineum*. Spearman analysis showed a negative correlation of median hatching date with average diel temperature for *S. flaveolum* ($n = 4$, $r_s = -0.2$, $p = 0.1$) and a positive correlation for *S. depressiusculum* ($n = 4$, $r_s = 0.4$, $p = 0.1$). In both species correlation was not significant, probably due to small sample size.

In each year hatching phenology of all 15 species differed significantly (two-sided Kruskal–Wallis test among species in each year, $p < 0.0001$, $\alpha = 0.01$) with a characteristic progression of the species investigated. *Sympetrum striolatum* and *S. meridionale* hatched to a great extent in the oviposition year. By keeping eggs in a dark refrigerator on moist filter paper, a facultative diapause could be induced. Eggs of *A. affinis*, *A. mixta*, *L. barbarus*, *L. dryas*, *L. macrostigma*, *L. sponsa*, *L. virens*, *L. viridis*, *S. danae*, *S. depressiusculum*, *S. flaveolum*, *S. sanguineum* and *S. vulgatum* showed an obligate diapause, which was interrupted only to some extent for a fraction of the eggs of *S. vulgatum* in one out of four study years (Figure 2, Figure 3) and in a few eggs of one clutch from *S. flaveolum*.

Larvae of the vernal pond species *A. affinis*, *L. barbarus*, *L. dryas* and *S. flaveolum* hatched in each year significantly earlier (two-sided Mann–Whitney U-test, $p < 0.0001$, $\alpha = 0.0005$) than those of the surveyed permanent pond species (Figures 2, 3). Seven of the 15 species hatched partly at temperatures below 5°C (Table 6). The lowest threshold temperature was observed in *L. barbarus*, from which on 22 January 2011 four larvae hatched at 1.1°C. Typical vernal pond

Table 5. Intraspecific variance of hatching events in clutches of different females. Vernal pond species are indicated in bold.

Species	Number of clutches	Oviposition date(s)	Number of tested combinations	Significant differences	
				Number of combinations	Rate of combinations (%)
<i>A. affinis</i>	7	8/14/ 21 August 2008	21	3	14
<i>S. flaveolum</i>	4	29 August– 1 September 2005	6	1	17
	2	16 July 2008	1	0	0
<i>A. mixta</i>	5	14/20/21/30 August 2008	10	8	80
<i>S. danae</i>	7	21 September 2007	21	2	10
	6	26 August 2008	15	7	47
<i>S. depressiusculum</i>	6	3 September 2005	15	4	27
	6	30 August, 3/5 September 2008	15	10	67

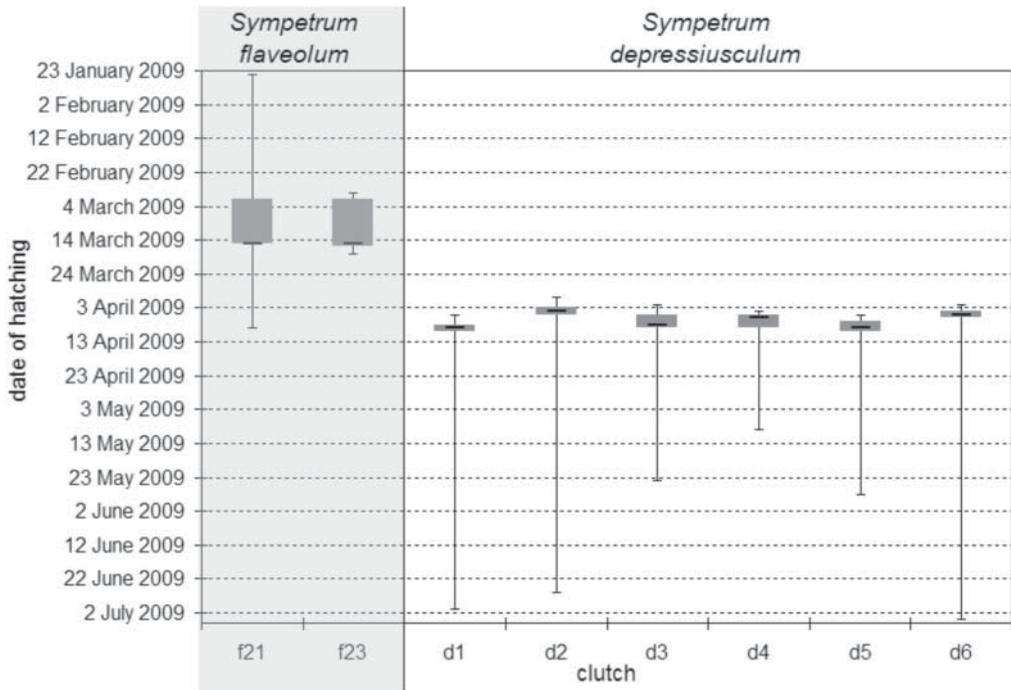


Figure 1. Intraspecific variance of hatching phenology. Boxplots showing maximum and minimum hatching date, quartiles 1, 3 and median hatching date of two clutches from different females of *Sympetrum flaveolum* (f21, f23) and six clutches from different females of *S. depressiusculum* (d1–d6) in 2009.

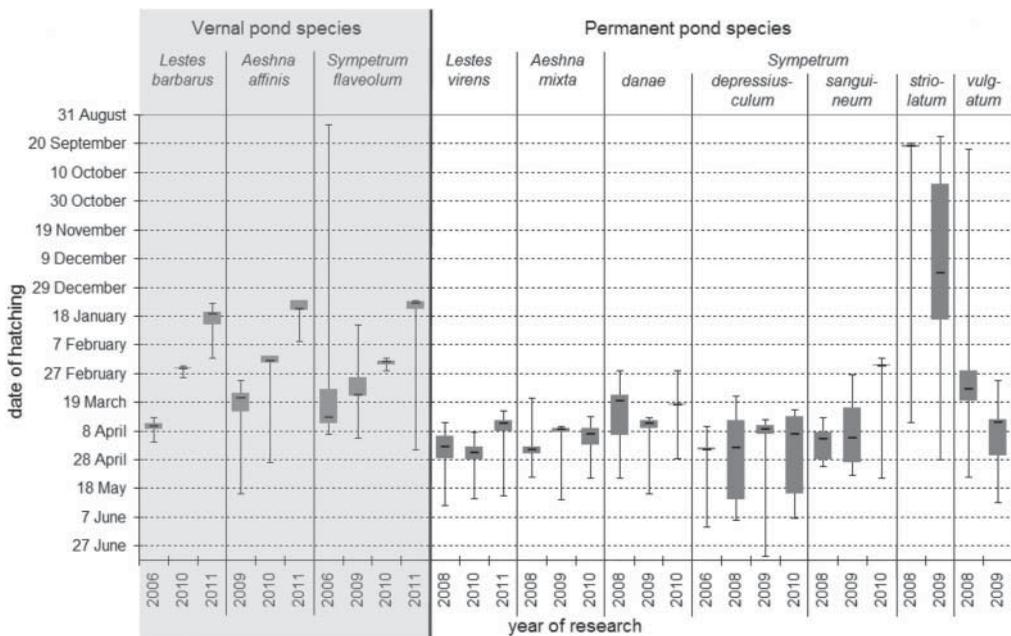


Figure 2. Annual variation in hatching phenology of 10 species in different years (boxplots showing maximum and minimum hatching date, quartiles 1, 3 and median). Vernal pond species are shaded.

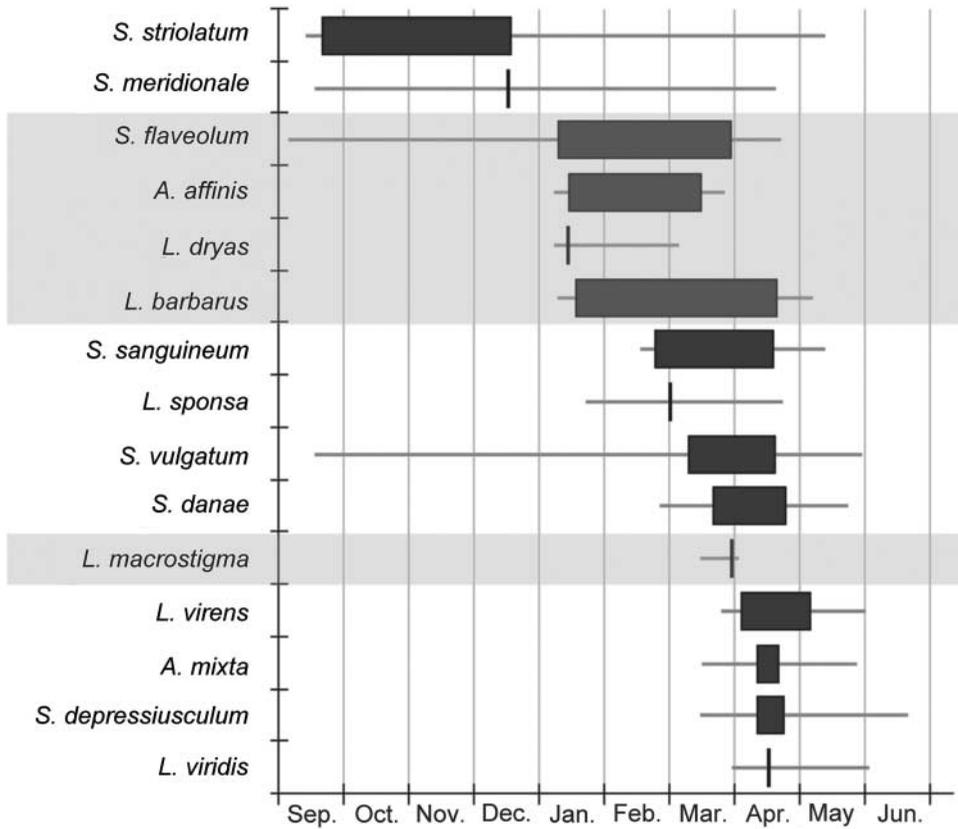


Figure 3. Hatching phenology of all 15 species in the study period from 2006 to 2011. Bars represent the time span between the maximum and minimum median hatching date. The lines show the complete time span of hatching. Vernal pond species are shaded.

Table 6. Minimum temperatures measured at hatching date and hatching rates at temperatures below 5°C and 10°C. Vernal pond species are indicated in bold.

Species	Minimum temperature measured (°C)	Date of minimum temperature	Hatching rates (%)		Number of hatchlings
			< 5°C	< 10°C	
<i>A. affinis</i>	3.2	16 February 2010	30	77	190
<i>L. barbarus</i>	1.1	24 January 2011	15	53	426
<i>L. dryas</i>	2.7	27 January 2011	10	51	242
<i>L. macrostigma</i>	12.4	27 March 2010	0	0	14
<i>S. flaveolum</i>	3.2	16 February 2010	2	63	187
<i>A. mixta</i>	5.6	2 April 2010	0	1	198
<i>L. sponsa</i>	1.7	22 January 2011	3	46	154
<i>L. virens</i>	8.3	6 Mai 2010	0	< 1	2138
<i>L. viridis</i>	13.8	13 April 2011	0	0	10,357
<i>S. danae</i>	5.9	14 March 2010	0	< 1	197
<i>S. depressiusculum</i>	8.3	6 May 2010	0	< 1	169
<i>S. meridionale</i>	8.3	17 December 2006	0	0	84
<i>S. sanguineum</i>	4.6	16 February 2010	1	25	190
<i>S. striolatum</i>	4.6	16 February 2010	1	23	163
<i>S. vulgatum</i>	5.4	17 March 2010	0	2	194

species *A. affinis*, *L. barbarus*, *L. dryas*, and *S. flaveolum* commonly hatched at low temperatures: hatching rates ranged from 51% to 77% at temperatures below 10°C and from 2% to 30% at temperatures below 5°C (Table 6).

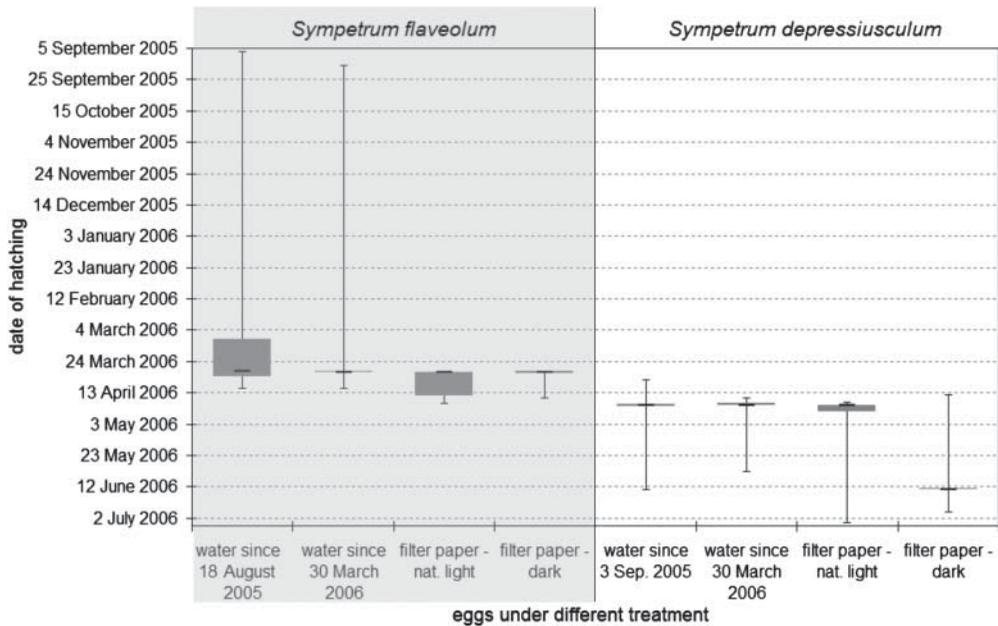


Figure 4. Effect of different egg treatments on hatching patterns of vernal pond species *Sympetrum flaveolum* (shaded) and permanent water species *S. depressiusculum*.

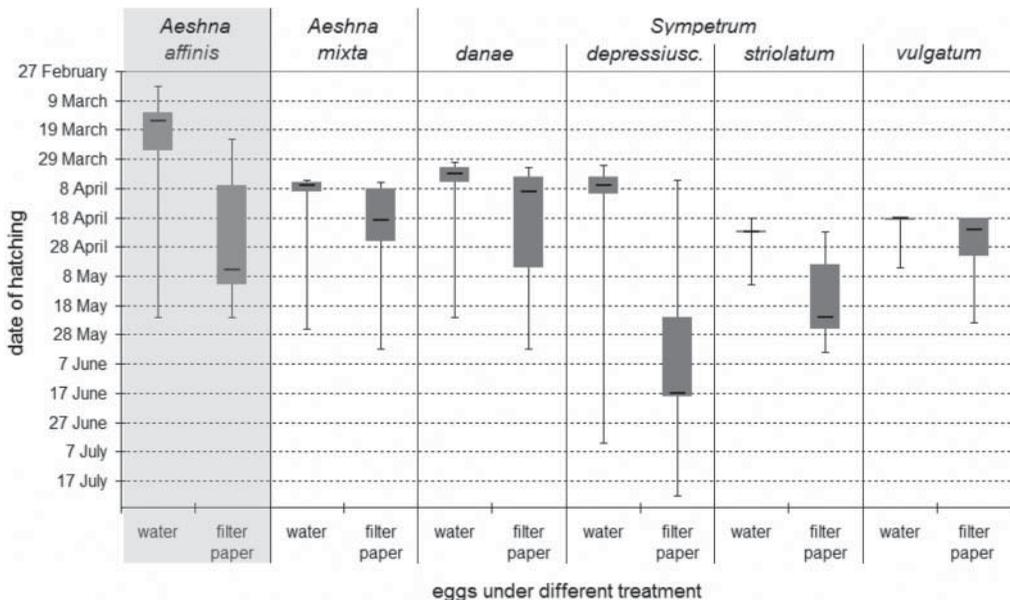


Figure 5. Effect of water cover versus moistened filter paper on hatching succession of eggs of vernal pond species *Aeshna affinis* (shaded) and permanent water species *A. mixta*, *Sympetrum danae*, *S. depressiusculum*, *S. striolatum*, and *S. vulgatum*.

Hatching delay

Hatching was delayed both in vernal pond species *A. affinis* and *S. flaveolum* and their permanent water congeners *A. mixta*, *S. danae*, *S. depressiusculum*, *S. striolatum* and *S. vulgatum* (two-sided

Table 7. Median hatching dates of eggs under different treatments. Vernal pond species are indicated in bold.

Species	Treatment			Time of delay between median dates (d)
	Water	Filter paper		
		Natural light	Dark	
<i>A. affinis</i>	16 March 2009	6 May 2009		51
<i>S. flaveolum</i>	30 March 2006	31 March 2006	31 March 2006	1 (1)*
<i>A. mixta</i>	7 April 2009	19 April 2009		12
<i>S. danae</i>	23 April 2007	26 May 2007		33
	3 April 2009	9 April 2009		6
<i>S. depressiusculum</i>	21 April 2006	21 April 2006	14 June 2006	0 (54)*
	23 April 2007	24 June 2007		62
	7 April 2009	17 June 2009		71
<i>S. striolatum</i>	23 April 2007	22 May 2007		29
<i>S. vulgatum</i>	18 April 2007	22 April 2007		4

*In parentheses: time of delay between median hatching dates from eggs on moist filter paper under natural light conditions and in the dark.

Table 8. Hatching success of eggs under different treatments. Vernal pond species are indicated in bold.

Species	Study year	Number of eggs			Hatching success (%)		
		Water	Filter paper		Water	Filter paper	
			Natural light	Dark		Natural light	Dark
<i>A. affinis</i>	2009	812	1032		91	6	
<i>S. flaveolum</i>	2006	325	321	270	98	22	15
<i>A. mixta</i>	2009	767	1994		89	90	
<i>S. danae</i>	2007	105	105		94	29	
	2009	634	1458		95	48	
<i>S. depressiusculum</i>	2006	321	317	321	94	63	1
	2007	737	741		96	21	
	2009	557	747		88	53	
<i>S. striolatum</i>	2007	520	132		95	39	
<i>S. vulgatum</i>	2007	1350	1105		93	53	

Mann–Whitney U-test for each species, $p < 0.0001$, $\alpha = 0.0005$) by keeping eggs on moist filter paper instead of water (Figure 4, Figure 5, Table 7).

Hatching of eggs of the vernal pond species *S. flaveolum* was not delayed by keeping them in the dark instead of keeping them under natural light conditions. In its permanent water congener *S. depressiusculum* hatching was significantly delayed by keeping eggs in the dark instead of keeping them under natural light conditions (Mann–Whitney U test, $p < 0.0001$, $\alpha = 0.0005$) (Figure 4).

The hatching patterns of *S. flaveolum* and *S. depressiusculum* of eggs kept in water from August/September 2005 and those transferred from moist filter paper into water in March 2006 did not differ significantly (two sided Mann–Whitney U-test, $p < 0.141$, $\alpha = 0.0005$) (Figure 4).

In six of the seven species hatching success was significantly higher for eggs in water than for eggs on moist filter paper (two-sided chi-square > 91.8 , $df = 1$, $p < 0.001$). Only in the permanent water species *A. mixta* there was no difference between hatching success of eggs placed in water compared to those kept on wet filter paper (two-sided chi-square = 1.9, $df = 1$, $p = 0.2$) (Table 8). For eggs of *S. flaveolum* and *S. depressiusculum* hatching success was significantly higher under natural light conditions than in the dark (two-sided chi-square > 4.3 , $df = 1$, $p < 0.05$) (Table 8).

Duration of egg survival

Although hatching was delayed by placing eggs on moist filter paper, survival of eggs for more than one year could not be proved under natural temperature conditions (Table 3); all eggs died.

Out of 603 eggs of *S. danae* from clutches oviposited in 2009 that were kept in a dark refrigerator at 5°C, only two larvae (0.3%) hatched in May 2011, and 215 (72%) out of 300 eggs of *S. depressiusculum*. Eggs of other surveyed species, including *A. affinis*, *L. barbarus*, *L. dryas* and *S. flaveolum*, placed in the refrigerator could not be kept alive for more than one year (Table 4).

Discussion

The purpose of this study was to find out if there are differences in the hatching patterns of temperate-centred species ecologically specialized in summer dry water bodies (vernal ponds) and species that are able to reproduce both in permanent and in temporary ponds. General mechanisms of seasonal regulation modes of hatching in temperate-centred Odonata species are already known. Hatching of species with direct egg development is mainly regulated by water temperature (Corbet, 1999; see also Pilon & Masseur, 1984), with development getting faster with increasing temperature. Referring to the thermal responses of egg development Pritchard, Harder, and Mutch (1996) found all 14 Odonata species in their analysis to be warm-adapted with a significantly smaller variance of thermal reaction norms than in other water insect groups. The authors concluded that temperate zone Odonata universally adopted diapause to synchronize cold sensitive stages with warm conditions (Pritchard et al., 1996). To protect the supposed cold-sensitive early larval stadia of univoltine species, which predominate in vernal ponds, from unsuitable low winter temperatures, many of these species exhibit delayed development with egg diapause; the latter can be terminated by water contact (e.g. Sawchyn & Gillot, 1974, for *Lestes congener*) and controlled by temperature (e.g. Boehms, 1971, for *S. vicinum*; Münchberg, 1933 for *L. sponsa*; Corbet, 1956a, for *L. sponsa*; Schaller, 1968, for *A. mixta*; Jinguji, Tujuzaki, & Ueda, 2010, for three *Sympetrum* spp.), and photoperiod (e.g. Sawchyn & Church, 1973, for *L. disjunctus* and *L. unguiculatus*; Śniegula & Johansson, 2010, for *L. sponsa*). These factors work together in a complex regulation scheme (reviewed in Corbet, 1999, p. 56) and are of different importance for various species. In non-diapause eggs and in pre- and post-diapause phase of diapause eggs development is positively correlated with temperature. In contrast, duration of diapause above a specific optimum temperature is negatively correlated with temperature (Boehms, 1971; Corbet, 1956a; Schaller, 1968). For example, the optimum temperature for diapause development was found to be near 10°C in *L. sponsa* (Corbet, 1956a), and in a range of 5 to 10°C in *A. mixta* (Schaller, 1968). In most species embryonic development is not static but may vary depending on environmental factors (see Boehms, 1971, for *S. vicinum*, Śniegula & Johansson, 2010, for *L. sponsa*). Embryonic development may also be genetically determined to some extent, as our own data presented here indicate and as was demonstrated by Śniegula & Johansson (2010) with eggs of *L. sponsa* originating from sites in Poland and Sweden.

Temperatures and, in consequence, hatching dates in natural habitats will differ from the semi-natural settings of this study: temperatures close to a building are one to two degrees higher than at a pond situated in an open landscape (own comparison of temperatures measured at the balcony with the ones measured by Deutscher Wetterdienst) and so hatching may have occurred earlier in this study than under field conditions. Nevertheless, as the conditions were identical for all 15 species studied, results comparing their hatching patterns can probably be transferred to the natural situation, and hatching data resulting from this study are similar to those of other authors for selected species (Table 9).

Table 9. Overview of published hatching dates of the investigated species, compared with the data of this study. Months without brackets represent the hatching span between quartiles 1 and 3; months in brackets represent minimum and maximum hatching data observed. Vernal pond species are indicated in bold.

Species	Data from this study		Literature		Sources
<i>A. affinis</i>	January to March	Diapause	March / April suspected	Diapause suspected	Bernard and Samolag (1997), Sternberg, Höppner, and Schmidt (2000)
<i>L. barbarus</i>	January to April (May)	Diapause	October to December, February / April	Diapause (sometimes direct)	Loibl (1958), Rota & Carchini (1988), Aguesse (1961–quoted after Sternberg & Röske, 1999)
<i>L. dryas</i>	January to (March)	Diapause	(November) March / April	Diapause (sometimes direct)	Needham (1903), Gardner (1952), Sawchyn and Church (1973), Wesenberg-Lund (1913)
<i>L. macrostigma</i> <i>S. flaveolum</i>	March (September) January to March (April)	Diapause Diapause (sometimes direct)	no data available Eggs oviposited in July/August hatching 8–10 weeks after oviposition, others hibernating in egg stage, April	No data available Egg-diapause depending on oviposition date	Jödicke (1997) Schiemenz (1953), Yokoyama (1999), Münchberg (1930)
<i>A. mixta</i>	March to April (May)	Diapause	March / April / May	Diapause	Schaller (1968, 1972), Gardner (1950c), Robert (1959)
<i>L. sponsa</i>	February / March (January to April)	Diapause	(September, October to December), April to June	Diapause	Loibl (1958), Wesenberg-Lund (1913), Münchberg (1933), Corbet (1956b), Śniegula & Johansson (2010)

(Continued).

Table 9. Continued

Species	Data from this study		Literature		Sources
<i>L. virens</i>	(March) April to May	Diapause	(October) End of April to End of May	Diapause	Münchberg (1933), Rota & Carchini (1988)
<i>L. viridis</i>	(March) April to (June)	Diapause	Beginning of April to Mid June	Diapause	Münchberg (1933), Loibl (1958), Sternberg (1999a), De Block, Stoks, and De Bruyn (2005)
<i>S. danae</i>	(February) March to April (May)	Diapause	(February) April to May	Diapause	Gardner (1951), Waringer (1983), Robert (1959), Yokoyama (1999)
<i>S. depressiusculum</i>	(March) April to (June)	Diapause	Mid April to Mid May	Diapause	Robert (1959)
<i>S. meridionale</i>	(September) December (April)	Direct	October to December	Direct (sometimes diapause suspected)	Aguesse (1959), Hoess (2003)
<i>S. sanguineum</i>	February to April (May)	Diapause	(October) April	Egg-diapause depending on oviposition date	Wesenberg-Lund (1913), Ottolenghi (1987), Gardner (1950a)
<i>S. striolatum</i>	September to December (May)	Direct (sometimes diapause)	September / October / November / January / February	Direct + diapause	Gardner (1950b), Ottolenghi (1987), Sternberg (1990), Corbet (1956b), Robert (1959), Cham (2006)
<i>S. vulgatum</i>	(September) March to April (May)	Diapause (sometimes direct)	April / May	Diapause	Münchberg (1930), Robert (1959)

Another methodological point that has to be discussed is the determination of minimum hatching temperatures and hatching rates below 5°C and 10°C. Because of the small size of the egg containers we assume that the air temperatures recorded next to them is close to the water temperatures inside of them. Nevertheless errors may result from the different heat capacity of water compared to air and a possible greenhouse heating inside the Petri dishes during very brief exposures to sunlight in the early morning in June after the main hatching season. Lastly, it was not possible to measure temperatures at the exact time of hatching. The minimum hatching temperatures we determined refer to the highest air temperatures measured in the time span between two hatching examinations. This means that minimum temperatures even could have been lower than indicated here. In spite of these reservations we consider our data as good approximations, especially with regard to comparing vernal pond species and their permanent water counterparts. Even if there is a high variance in egg hatching patterns between clutches of one year laid by various females of one species, which suggests a high genotypic impact of hatching phenology, this study reveals a high degree of hatching synchronization and species-specific hatching patterns with a characteristic hatching succession shown by the species studied here (Figure 3, Table 9). However, hatching patterns of single species differed significantly between different study years. This can more likely be attributed to different temperature conditions of the different study years than to the photoperiod, although day length may play an important role for egg sensitivity to rising temperatures. In *S. flaveolum* we found a negative correlation between average diel temperatures and median hatching date, and in *S. depressiusculum* a positive correlation, which was in both cases not significant probably due to small sample size.

In *L. barbarus* and *A. affinis* our data also suggest a negative correlation between median hatching date and average diel temperatures similar to those in *S. flaveolum*. This suggests a significant influence of temperature patterns in hatching phenology of early hatching vernal pond species, whereas hatching patterns of late hatching permanent pond species seem to be less influenced by average diel temperatures. The influence of day length in triggering hatching was already shown for *L. disjunctus*, *L. unguiculatus* and *L. dryas* in Canada (Sawchyn & Church, 1973) and by Śniegula & Johansson (2010) for *L. sponsa* in Europe. The latter species hatched earlier in longer photoperiods, typical for higher latitudes (Śniegula & Johansson, 2010). Species with life cycles adapted to a Mediterranean or oceanic climate, such as *S. meridionale* (Aguesse, 1959; Hoess, 2003; our unpublished data) and *S. striolatum* (Cham, 2006; Gardner, 1950b; Ottolenghi, 1987; Sternberg, 1990; our data), usually show direct embryonic development and typically hatch 10 to 16 days after oviposition. Usually *S. striolatum* overwinters in larval stadium 2 to 6 (Corbet, 1956b) and continues development in the next spring. This species may be bivoltine even under temperate climate conditions, as was shown by Jödicke & Thomas (1993). On the other hand, eggs of *S. striolatum* can exceptionally show a delayed development with diapause if oviposited late in autumn (Ottolenghi, 1987; Robert, 1959) with the larvae hatching 80 to 184 days after oviposition. As shown in this study, keeping the eggs in the refrigerator may have induced delayed development, and hatching of most eggs could be postponed. Delayed development of *S. meridionale* and *S. striolatum* eggs may occur in clutches with a late oviposition date and under temperate climate conditions with winter temperatures falling below a variable threshold temperature (our data; for *S. striolatum* see also Ottolenghi, 1987; Robert, 1959).

All other studied species typically show delayed embryonic development with winter diapause and hatching in the spring after oviposition. In rare cases, however, some larvae may already hatch in autumn of the oviposition year. This has been shown for *S. sanguineum* (Gardner, 1950a; Wesenberg-Lund, 1913), *S. flaveolum* (Obana, 1974, quoted by Corbet, 1999; our data), *S. vulgatum* (our data), *L. dryas* (Gardner, 1952 – seminatural conditions; Needham, 1903), *L. barbarus* and/or *L. virens* (Rota & Carchini, 1988, SE Italy; for *L. barbarus* also Loibl, 1958 – laboratory) and *L. sponsa* (Münchberg, 1933; Warren, 1988).

Among species with obligate egg diapause, those adapted to vernal ponds – *A. affinis*, *S. flaveolum*, *L. dryas*, and *L. barbarus* – hatched significantly earlier in the course of the year than species less adapted to this specific type of water, namely *A. mixta*, *S. danae*, *S. depressiusculum*, *S. sanguineum*, *S. vulgatum*, *L. macrostigma*, *L. sponosa*, *L. virens*, and *L. viridis*. Hatching of four vernal pond species occurred to a remarkably high extent at temperatures between 0°C and 5°C. This is contradictory to the assumption that high thermal coefficients are mandatory for the development of *A. affinis* and *L. barbarus*, which are often assigned to be “southern” species adapted to a Mediterranean climate (e.g. Sternberg & Röske, 1999; Sternberg et al., 2000). The only exception is *L. macrostigma*. This species is a characteristic inhabitant of vernal ponds as well, but has a more southern range, reaching central Europe only in the south-eastern part of Austria (Jödicke, 1997), where climate is subcontinentally warm, and probably higher temperatures are needed for larval development.

All other species of this study reproduce either both in temporary and permanent waters or, in the case of *S. depressiusculum*, are confined to inundation areas influenced by nival water regimes as primary habitats. Here, the highest water levels are reached when snow is melting in alpine areas – in central Europe between May and July (Sternberg & Schmidt, 2000). All these species hatch later. Consequently, phenologically early hatching can be regarded as an adaptation allowing typical vernal pond species the completion of larval development before the larval habitats dry out. De Block et al. (2005) even found different hatching patterns amongst populations of *L. viridis* in Belgium, with populations inhabiting temporary waters hatching earlier than those reproducing in permanent ponds.

Reproduction in vernal ponds may be a strategy to avoid competition with and predation by congeners and other predators developing in semipermanent or permanent waters (Stoks & McPeck, 2003). For typical species of vernal ponds, the avoidance or at least reduction of predation and competition by other species apparently outweighs the great disadvantage that the duration of water coverage is unpredictable. To cope with the risk of early drying-up of the larval habitats, one adaptation of these species is early hatching.

Hatching could be delayed by keeping eggs on moist filter paper instead of putting them into water, the latter working as a hatching stimulus (Figures 4, 5). To a certain extent all studied species were capable of delaying the time of hatching, without any difference between vernal pond and permanent water species. The strongest differences of median hatching dates were observed in *S. depressiusculum* eggs. Their median hatching date was delayed up to 71 days in 2009 (Figure 5, Table 7). On the other hand, the delayed hatching resulted in significantly lower hatching success in all species except *A. mixta* (Table 8). However, the ability to delay hatching in the absence of water is a chance for at least a fraction of the eggs to survive an extraordinary winter drought period, a phenomenon already described by Arai (1984) who observed that winter drought led to delayed hatching of overwintering eggs of *Sympetrum* spp. in a dried-up swamp.

There are some indications that diapause eggs live more than one year. The option to survive for more than one year is supposed to be an appropriate adaptation to unforeseeable water availability, which is a characteristic quality in vernal ponds. Sternberg (1999b) reports that 0.4–1.5% of *L. sponosa* eggs did not hatch in the spring after oviposition but in the second year, thus having overwintered two times. Röhn, Sternberg, and Kuhn (1999, p. 406) report hatching of *L. dryas* in August and October in the first year after oviposition, which is an indication of the capacity to hatch in the second year after oviposition in order to survive an unsuitable year for larval development in the egg stage. The ability to survive unsuitably dry years in diapause is also hypothesized for *A. affinis* (Sternberg et al., 2000), *S. depressiusculum* (Sternberg & Schmidt, 2000), and *S. flaveolum* (Röhn, Kuhn, & Sternberg, 2000). However, in our study no eggs of either typical vernal pond species or of their permanent water congeners survived more than one season under seminatural conditions. Nevertheless, a high hatching success of 72% of

S. depressiusculum eggs that had been kept in the refrigerator in the second year after oviposition implies that at least for this species, under special conditions, a survival of eggs for more than one year might be possible. Altogether our results suggest that survival of eggs for more than one year occurs only exceptionally.

In summary, our study contributes to the knowledge of adaptations of vernal pond Odonata species to the specific ecological factor of abbreviated water coverage of their larval habitats. De Block & Stoks (2004, 2005) and De Block et al. (2005) have already demonstrated for *L. viridis* that early hatching is a possible strategy to complete larval development in temporary waters before these waters dry out. In a comparative approach with 15 Odonata species from three families we demonstrated that phenologically early hatching is a common strategy in vernal pond Odonata to cope with the unpredictability of water coverage in their larval habitats. As our data suggest, timing of hatching of vernal pond species is negatively correlated with average diel temperatures. This enables vernal pond species to hatch earlier in warmer years and improve their chance to complete aquatic development before larval habitats dry out.

We found that hatching was delayed in both vernal and permanent pond species when eggs experienced an experimental drought on moist filter paper. This strategy worked only over a short time span of several weeks and was – with the exception of the permanent water species *A. mixta* – connected with greatly reduced hatching success. This result, in accordance with our persistence experiments, suggests that survival of eggs for more than one year is not a strategy used by European vernal pond species to endure at vernal ponds during drought years. Such vernal pond habitats probably have to be recolonized following extinction. This is a typical trait of species forming metapopulations. In terms of species protection, our results underline the importance of maintaining or re-establishing networks of vernal pond habitats.

Our knowledge about the adaptations of vernal pond Odonata species is still insufficient. Questions that should be tackled experimentally include, amongst others, how vernal pond species differ from their permanent-water-dwelling counterparts in different aspects of larval ecology such as duration of larval development, number of larval stadia, and larval life styles.

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References

- Addinsoft. (2014). XLSTAT-Pro, Version 2014.4.04. Paris: Addinsoft SARL.
- Aguesse, P. (1959). Notes biologiques sur l'éclosion des œufs de quelques Libellulidae. *La Terre et la Vie*, 1959, 165–173.
- Aguesse, P. (1961). *Contribution à l'étude écologique des zygoptères de Camargue* (PhD thesis). Université de Paris, Paris.
- Arai, Y. (1984). Notes on the survival of dragonfly in dried up swamps. *Tombo*, 27, 32–34 [In Japanese with English abstract].
- Bernard, R., & Samolag, J. (1997). Analysis of the emergence of *Aeshna affinis* Vander Linden, 1823 in the Vicinity of Poznań, Western Poland (Odonata: Aeshnidae). *Opusculae zoologicae fluminensis*, 153, 1–12.
- Boehms, C. (1971). *The influence of temperature upon embryonic diapause and seasonal regulation in Sympetrum vicinum (Hagen) (Odonata: Libellulidae)* (PhD thesis). University of North Carolina, Chapel Hill, NC, USA.
- Cham, S. (2006). Development and hatching of eggs of the Common Darter, *Sympetrum striolatum* (Charpentier). *Journal of the British Dragonfly Society*, 22, 36–40.
- Corbet, P. S. (1956a). The influence of temperature on diapause development in the dragonfly *Lestes sponsa* (Hansemann) (Odonata: Lestidae). *Proceedings of the Royal Entomological Society of London (A)*, 31, 45–48.
- Corbet, P. S. (1956b). The life histories of *Lestes sponsa* (Hansemann) and *Sympetrum striolatum* (Charpentier) (Odonata). *Tijdschrift voor Entomologie*, 99, 217–229.
- Corbet, P. S. (1999). *Dragonflies. Behaviour and ecology of Odonata*. Colchester: Harley Books.

- De Block, M., & Stoks, R. (2004). Life-history variation in relation to time constraints in a damselfly. *Oecologia*, *140*, 68–75. doi:10.1007/s00442-004-1575-6
- De Block, M., & Stoks, R. (2005). Pond drying and hatching date shape the trade-off between age and size at emergence in a damselfly. *Oikos*, *180*, 485–494.
- De Block, M., Stoks, R., & De Bruyn, L. (2005). Egg hatching patterns within and among populations of a damselfly occupying permanent and temporary ponds. *Archiv für Hydrobiologie*, *163*, 195–209. doi:10.1127/0003-9136/2005/0163-0195
- Gardner, A. E. (1950a). The life-history of *Sympetrum sanguineum* (Müller) (Odonata). *Entomologist's Gazette*, *1*, 21–26.
- Gardner, A. E. (1950b). The life-history of *Sympetrum striolatum striolatum* (Charpentier) (Odonata). *Entomologist's Gazette*, *1*, 53–60.
- Gardner, A. E. (1950c). The life-history of *Aeshna mixta* Latreille (Odonata). *Entomologist's Gazette*, *1*, 128–138.
- Gardner, A. E. (1951). The life-history of *Sympetrum danae* (Sulzer) = *S. scoticum* (Donovan) (Odonata). *Entomologist's Gazette*, *2*, 109–127.
- Gardner, A. E. (1952). The life-history of *Lestes dryas* Kirby (Odonata). *Entomologist's Gazette*, *3*, 4–26.
- Hoess, R. (2003). Ist *Sympetrum meridionale* in der Schweiz heimisch? Funde von 1998–2002 und Anmerkungen zu Habitat, Phänologie, Verhalten und Morphologie (Odonata: Libellulidae). *Libellula*, *22*, 61–86.
- Jinguiji, H., Tujuzaki, H., & Ueda, T. (2010). Effects of temperature and light on the hatching of overwintering eggs in three Japanese *Sympetrum* species. *Paddy and Water Environment*, *8*, 385–391. doi:10.1007/s10333-010-0217-3
- Jödicke, R. (1997). *Die Binsenjungfern und Winterlibellen Europas*. Magdeburg: Westarp Wissenschaften.
- Jödicke, R., & Thomas, B. (1993). Bivoltine Entwicklungszyklen bei *Sympetrum striolatum* (Charpentier) in Mitteleuropa (Anisoptera: Libellulidae). *Odonatologica*, *22*, 357–364.
- Loibl, E. (1958). Zur Ethologie und Biologie der deutschen Lestiden (Odonata). *Zeitschrift für Tierpsychologie*, *15*, 54–81.
- Münchberg, P. (1930). Beiträge zur Kenntnis der Biologie der Odonaten Nordostdeutschlands. Die Biologie des Genus *Sympetrum* Newm. *Sitzungsberichte der Gesellschaft Naturfreunde Berlin*, *5*, 205–234.
- Münchberg, P. (1933). Beiträge zur Kenntnis der Biologie der Lestinae Calv. *Internationale Revue der gesamten Hydrobiologie und Hydrographie Leipzig*, *28*, 141–171.
- Needham, J. G. (1903). Aquatic insects in New York State. Part 3. Life histories of Odonata, suborder Zygoptera. *New York State Museum Bulletin*, *68*, 204–217.
- Obana, S. (1974). Duration of the egg stage in dragonflies. *Gracile*, *16*, 1–3 [In Japanese].
- Ottolenghi, C. (1987). Reproductive behaviour of *Sympetrum striolatum* (Charp.) at an artificial pond in northern Italy (Anisoptera: Libellulidae). *Odonatologica*, *16*, 297–306.
- Pilon, J. G. & Masseau, M. J. (1984). The effect of temperature on egg development in Zygoptera: a preliminary discussion. *Advances in Odonatology*, *2*, 177–193.
- Pritchard, G., Harder, L. D., & Mutch R. A. (1996). Development of aquatic insect eggs in relation to temperature and strategies for dealing with different thermal environments. *Biological Journal of the Linnean Society*, *58*, 221–244. doi:10.1111/j.1095-8312.1996.tb01432.x
- Robert, P.-A. (1959). *Die Libellen (Odonaten)*. Bern: Kümmerly & Frey.
- Röhn, C., Sternberg, K., & Kuhn, J. (1999). *Lestes dryas* (Kirby, 1890). In K. Sternberg & R. Buchwald (Eds.), *Die Libellen Baden-Württembergs Volume 1* (pp. 398–408). Stuttgart: Ulmer.
- Röhn, C., Kuhn, J., & Sternberg, K. (2000). *Sympetrum flaveolum* (Linnaeus, 1758). In K. Sternberg & R. Buchwald (Eds.), *Die Libellen Baden-Württembergs Volume 2* (pp. 548–559). Stuttgart: Ulmer.
- Rota, E., & Carchini, G. (1988). Considerations on an autumn record of *Lestes* larvae in Italy (Zygoptera: Lestidae). *Notulae Odonatologicae*, *3*, 9–13.
- Sawchyn, W. W., & Church, N. S. (1973). The effects of temperature and photoperiod on diapause development in the eggs of four species of *Lestes* (Odonata: Zygoptera). *Canadian Journal of Zoology*, *51*, 1257–1265.
- Sawchyn, W. W., & Gillott, C. (1974). The life history of *Lestes congener* (Odonata: Zygoptera) on the Canadian Prairies. *The Canadian Entomologist*, *106*, 367–376.
- Schaller, F. (1968). Action de la température sur la diapause et le développement de l'embryon d'*Aeshna mixta* (Odonata). *Journal of Insect Physiology*, *14*, 1477–1483.
- Schaller, F. (1972). Action de la température sur la diapause embryonnaire et sur le typ de développement d'*Aeshna mixta* Latreille (Anisoptera: Aeshnidae). *Odonatologica*, *1*, 143–153.
- Schiemenz, H. (1953). *Die Libellen unserer Heimat*. Jena: Schriener.
- Śniegula, S., & Johansson, F. (2010). Photoperiod affects compensating developmental rate across latitudes in the damselfly *Lestes sponsa*. *Ecological Entomology*, *35*, 149–157. doi:10.1111/j.1365-2311.2009.01164.x
- Sternberg, K. (1990). *Autökologie von sechs Libellenarten der Moore und Hochmoore des Schwarzwaldes und Ursachen ihrer Moorbundung* (PhD thesis). Albert-Ludwigs-Universität, Freiburg i. Br., Germany.
- Sternberg, K. (1999a). *Chalcolestes viridis* (Vander Linden, 1825). In K. Sternberg & R. Buchwald (Eds.), *Die Libellen Baden-Württembergs Volume 1* (pp. 379–388). Stuttgart: Ulmer.
- Sternberg, K. (1999b). *Lestes sponsa* (Hansemann, 1823). In K. Sternberg & R. Buchwald (Eds.), *Die Libellen Baden-Württembergs Volume 1* (pp. 409–418). Stuttgart: Ulmer.
- Sternberg, K., Höppner, B., & Schmidt, B. (2000). *Aeshna affinis* Vander Linden, 1820. In K. Sternberg & R. Buchwald (Eds.), *Die Libellen Baden-Württembergs Volume 2* (pp. 8–23). Stuttgart: Ulmer.
- Sternberg, K. & Röske, W. (1999). *Lestes barbarus* (Fabricius, 1798). In K. Sternberg & R. Buchwald (Eds.), *Die Libellen Baden-Württembergs Volume 1* (pp. 388–398). Ulmer: Stuttgart.

- Sternberg, K., & Schmidt, B. (2000). *Sympetrum depressiusculum* (Sélys, 1841). In K. Sternberg & R. Buchwald (Eds.), *Die Libellen Baden-Württembergs Volume 2*: (pp. 534–548). Stuttgart: Ulmer.
- Stoks, R., & McPeck, M. A. (2003). Predators and life histories shape *Lestes* damselfly assemblages along a freshwater habitat gradient. *Ecology*, *84*, 1576–1587. Retrieved from [http://dx.doi.org/10.1890/0012-9658\(2003\)084\[1576:PALHSL\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2003)084[1576:PALHSL]2.0.CO;2)
- Suhling, F., Jödicke, R., & Schneider, W. (2003). Odonata of African arid regions – are there desert species? *Cimbebasia*, *18*, 207–224.
- Suhling, F., Schenk, K., Padeffke, T., & Martens, A. (2004). A field study of larval development in a dragonfly assemblage in African desert ponds (Odonata). *Hydrobiologia*, *528*, 75–85.
- Waringer, J. (1983). A study on embryonic development and larval growth of *Sympetrum danae* (Sulzer) at two artificial ponds in lower Austria (Anisoptera: Libellulidae). *Odonatologica*, *12*, 331–343.
- Warren, P. H. (1988). Larval overwintering in *Lestes sponsa* (Hans.) (Zygoptera: Lestidae). *Notulae odonatologicae*, *3*, 15–16.
- Wesenberg-Lund, C. (1913). Odonaten-Studien. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, *6*, 155–228, 373–422.
- Yokoyama, T. (1999). Notes on the durations of the egg stages on some dragonflies in Hokkaido 2. *Aeshna*, *37*, 22–26 [In Japanese with English abstract].